

**Studies in Dedifferentiation. IV. Resorption
and Differential Inhibition in Obelia and
Campanularia.**

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With Plate 26 and 7 Text-figures.

INTRODUCTION.

It is well known that among the processes whereby an organism is developed all are not constructive, but some may involve the demolition of certain structures which may either have ceased to subserve a useful function, or may actually hinder further development. A familiar example is the gill or tail of Amphibian larvae at metamorphosis.

In normal circumstances this retrogression only affects certain organs, but recently it has been found possible to produce this effect experimentally in whole organisms (Driesch, 1906, &c.).

Protozoa, Planarians, Sponges, Ascidians, and Coelenterates will under certain conditions give the retrogressive effect, as evidenced by the work of Lund (1917), Child (1904), Maas (1910), Huxley (1921 *b*), Loeb (1900), and others.

Following some observational work by one of us (J.S.H.), it was thought that quantitative experiments involving the subjection of organisms to different concentrations of poisons might give interesting results. One of the authors (G.R. de B.) accordingly performed some experiments on *Obelia geniculata* which will be described below.

The Hydrozoa are not virgin soil to the experimentalist in this connexion. Loeb (1900) observed that under certain conditions the zooids of a hydroid colony would lose all their shape and structure and retreat into the hydrocaulus. He attributed the cause of this to contact with solid objects, viz. the watch-glass in which the organisms were kept; but this explanation is probably not correct.

Thacher (1903) investigated the process of retrogression in hydroids and called it 'absorption'. Cerfontaine (1902) says of it: 'les individus . . . dégènèrent et disparaissent.' Gast and Godlewski (1903) merely called it 'degeneration' ('Rückbildungsprozess'). These terms are inadequate to designate a process as specific as that which Huxley (1921*b*) has described in the case of *Perophora*. Strictly speaking, there are two processes at work, viz. dedifferentiation and resorption. In the following description of the experiments performed Resorption will be used to mean the process whereby the material composing the zooid is transported, and Dedifferentiation to mean other processes undergone involving a return of cells or tissues to a simpler, less differentiated condition.

In the organisms chosen for experiment there is a coëxistence of two sets of systems, the 'zooid systems' and the 'stolon systems'. It is obvious that normally physiological equilibrium must exist between them. But if circumstances can be found whereby one system is adversely affected more than the other there will occur differential inhibition associated with resorption or dedifferentiation or both.

The experiments were performed at the Biological Laboratory, Woods' Hole, in 1916 (*Campanularia*, J.S.H.), and at the Marine Biological Laboratory, Plymouth, in 1920 (*Obelia*, G.R. de B.).

EXPERIMENTAL.

Given the fact that mere subjection to unfavourable conditions, viz. being kept in glass vessels in the laboratory, brings about resorption of zooids in hydroids, it was to be expected that if the toxicity of the water were increased, the process of

resorption would be accelerated and the differential inhibition made more specific. Apart from their plentifulness, *Obelia* and *Campanularia* are suitable material because :

- (i) The zooids are conveniently far apart and attached to the hydrocaulus by a fairly long stem ;
- (ii) The zooids in their natural condition are highly differentiated structures compared with the rest of the colony ;
- (iii) The stages of resorption can be conveniently determined by reference to the hydrotheca.

On the other hand there is the disadvantage that it has poor viability, which means that resorption takes place even in the controls in clean sea-water. This, however, occurs long after it has done so in the toxic solutions.

Care was taken to ensure that the colonies were clean and healthy and free from Diatoms and Protozoa, and that all the polyps were normal and fully extended.

The experimental solutions are referred to in terms of concentrations of KCN ; but since the solvent was sea and not pure water such an expression as $\frac{N}{10}$ does not give us the actual ionic concentration.

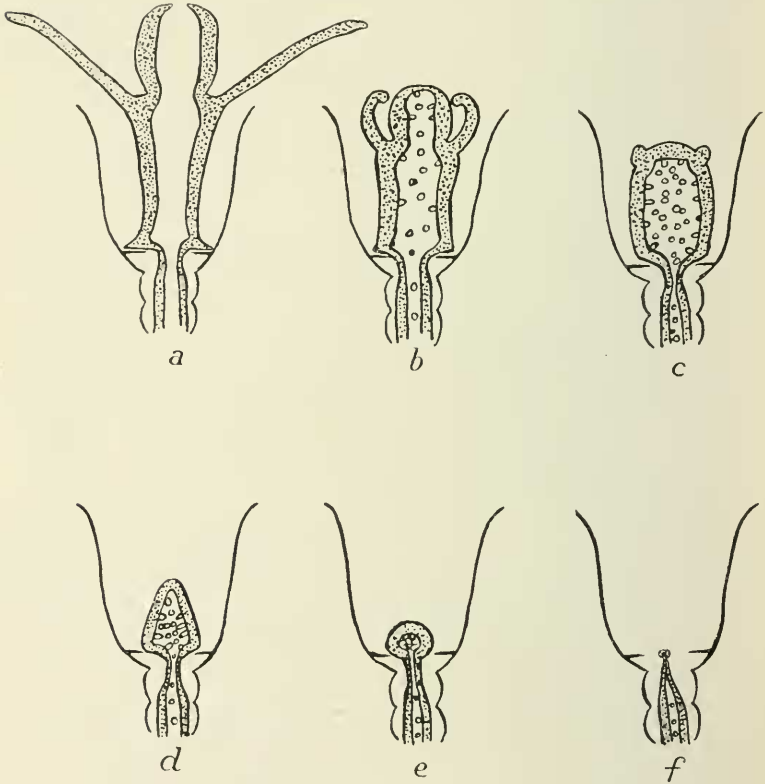
The solutions were made up in shallow glass dishes, in each of which a small number of stems of *Obelia* each bearing eight zooids (Table I) or one zooid (Tables II to IV) were placed. In every case the material used was fresh from the sea. KCN solutions were kept covered owing to the volatile nature of KCN, and changed every day.

Resorption can be divided into five stages (Text-fig. 1). Text-fig. 1, *a*, represents a normal zooid (also Pl. 26, fig. 1).

First Stage. The tentacles are first affected. They may become apposed to the hypostome, and may shrink so as to become shorter than the hypostome. Adjacent tentacles may fuse (Pl. 26, fig. 9), indicating an interesting change in consistency. The mouth closes, but the hypostome is still prominent. Ciliary action continues in the enteron as in the normal zooid (Text-fig. 1, *b*, and Pl. 26, figs. 2 and 3).

Second Stage. The hypostome is completely resorbed and the tentacles are represented only by a ring of tiny prominences. The 'waist' in the body of the zooid has disappeared. The whole is well within the margin of the hydrotheca. The stalk

TEXT-FIG. 1.



Diagrams representing: *a*, normal zooid; *b*, first, *c*, second, *d*, third, *e*, fourth, *f*, fifth stages of resorption remaining in the hydrotheca.

attaching the zooid to the hydrocaulus is very thin and within it is a mass of cells and débris flowing slowly away from the zooid (Text-figs. 1, *c*, and 2).

Third Stage. The zooid has shrunk towards the bottom

of the hydrotheca; its shape is roughly ovoid. No sign of tentacles whatsoever (Text-figs. 1, *d*, and 3, *a*, and Pl. 26, fig. 4).

Fourth Stage. Sometimes the distal portion of the zooid may become separated from the rest (Text-fig. 4). The form-determining properties of the zooid have become less powerful than the surface tension acting upon it, and it has accordingly become spherical, nowhere touching the hydrotheca and connected by a thin stalk to the hydrocaulus. At this stage and later the flow in the tube is irregular. It appears to be maintained by pulsations of the stolon (see p. 479) (Text-fig. 1, *e*, and Pl. 26, fig. 5).

Fifth Stage. The process has been continued until the zooid is represented only by a tiny knob (often containing pigment) smaller in diameter than the hydrocaulus (Text-figs. 1, *f*, and 5). Occasionally the process is carried further and the hydrotheca becomes empty. This only occurs a considerable time after stage 5, and is mainly a mere degeneration effect.

It should be noted that in those cases where the colonies contained gonothecae, medusae were not liberated if resorption had started. During resorption the zooids are perfectly healthy and transparent. Dead tissues can always be distinguished (opacity, &c.). Small masses of dense pigment are often found in the partly resorbed zooid, representing products of degeneration.

As resorption goes on, the material derived from the zooid passes into the hydrocaulus, and from the proximal (cut) end of the latter a stolon begins to grow (Text-fig. 3, *a* and *c*). It is very transparent and clear, and may grow to the length of 10 mm. or more, affixing itself to the substratum. It sometimes happens that a small portion of what is left of the zooid in stages 3-5 is completely nipped off (by surface tension) from the hydrocaulus. It remains in the hydrotheca and dies (Text-fig. 4).

In the earlier experiments the solutions used were too strong, but even so a differential effect was obtained (Table I).

TABLE I (Obelia).

Strength of KCN.						
N/2,000	Dead					
N/4,000		Dead				
N/8,000			Dead			
N/16,000				Dead		
N/32,000			I	II	Dead	
N/64,000				I	II	
Controls Sea-water				Quite healthy		I
	3	10	15	20	25	30 hours.

The Roman figures denote the stage of resorption at a particular time in a solution of given strength. All solutions up to N/32,000 are too strong and kill the organisms before any resorption occurs: in the N/32,000 solution resorption proceeded a little way but the organisms were then overcome by the poison.

It soon became apparent that the preparations used were not wholly satisfactory, for of the eight zooids borne by the colonies all had not been resorbed to the same extent at the same time. To meet this difficulty portions of the hydrocaulus were used bearing only one well-expanded zooid.

TABLE II (Obelia).

After : In	6 hours.	10 hours.	24 hours.	36 hours.
N/8,000	All dead			
N/16,000	All dead			
N/32,000	Stage I	All dead		
N/64,000	Trace of resorption	Stages I and II	All dead	
Control	Expanded and motile	Expanded and motile	Trace of resorption	Stages I and II.

The results of this experiment were much more definite, but the solutions used were still too strong.

TABLE III (Obelia).

<i>After :</i> <i>In</i>	16 hours.	24 hours.	40 hours.	50 hours.
N/64,000	Stage II. No medusae liberated	Dead		
N/128,000	Stage I. No medusae liberated	Stages II and III	Dead	
N/256,000	Trace of resorption. A few medusae liberated	Stages I and II	Stages III and IV	Stage V and Dead
Controls	Fully expanded. Several medusae liberated	Traces of resorption	Stages I and II	Stage III.

Experiments in the N/256,000 solution were repeated several times with the same results. These results indicate that a N/256,000 solution of KCN inhibits the zooids without affecting the hydrocaulus to any appreciable extent (at least for a considerable time—fifty hours). The healthy nature of the hydrocaulus is evidenced by movements of contraction and pulsation, and by growth at the proximal extremity.

The contraction of the stem is of interest, since precisely similar contraction occurs in *Perophora* and other *Ascidians* (Huxley, 1921 *b*). In addition, the partly dedifferentiated zooid also appears to contract at intervals (Text-fig. 3), although it is possible that the contraction is a mere surface-tension effect, exerted passively on relaxation of the walls of the stem. It appears that the contraction of the cells of the stem occurs when considerable internal tension has been produced through the flow of liquid and cells from the zooid. In higher forms embryonic cells which are destined to give rise to muscle appear to start contracting before differentiation, also as a result of tension (e.g. Carey, 1921 *a* and 1921 *b*, &c.).

It is possible that contraction produced by tension has no normal function in hydroid stems. It is all the more interesting to find that it occurs, being thus probably a general property of all not too highly-differentiated cells. Possibly tension acts also as a stimulus to outgrowth from the stem. (Cf. the well-known fact of better growth in regenerating *Tubularia* in hypotonic sea-water (Loeb, 1892).)

In order to see whether any of the results obtained were due to the specific effects of KCN, experiments were also made with HgCl_2 . When solutions of N/1,000,000 and N/2,000,000 were used, the resorption effects were identical with those in KCN.

TABLE IV (Obelia).

		<i>After 24 hours.</i>
KCN	$\frac{\text{N}}{128,000}$. . .	Stages II and III.
	$\frac{\text{N}}{256,000}$. . .	Stage I.
HgCl_2	$\frac{\text{N}}{10^6}$. . .	Half dead, remainder Stage III.
	$\frac{\text{N}}{2 \times 10^6}$. . .	Stage I.
Control	. . .	Fully expanded.

After varying periods in solutions of all the strengths, some preparations were removed and placed in clean fresh sea-water with a view to inducing them to cease resorption and reform zooids. In no case was this successful. The preparations ceased resorption for a short time, but then continued. This was to be expected from the behaviour of zooids in normal sea-water.

When the zooid is severed from the stem at the base of the hydrotheca, the preliminary dedifferentiation occurs as usual; but after a certain number of cells have migrated into the interior there is no room for more. The result is an ovoid dedifferentiated mass, tightly packed with cells (Text-fig. 6). Similar phenomena were seen in *Perophora*. Thus the degree of resorption depends on the amount of space available. Resorption will only proceed to a limit when the migrating cells are removed. A parallel is here provided with those chemical reactions which will only proceed to a limit if the products of the reaction are removed.

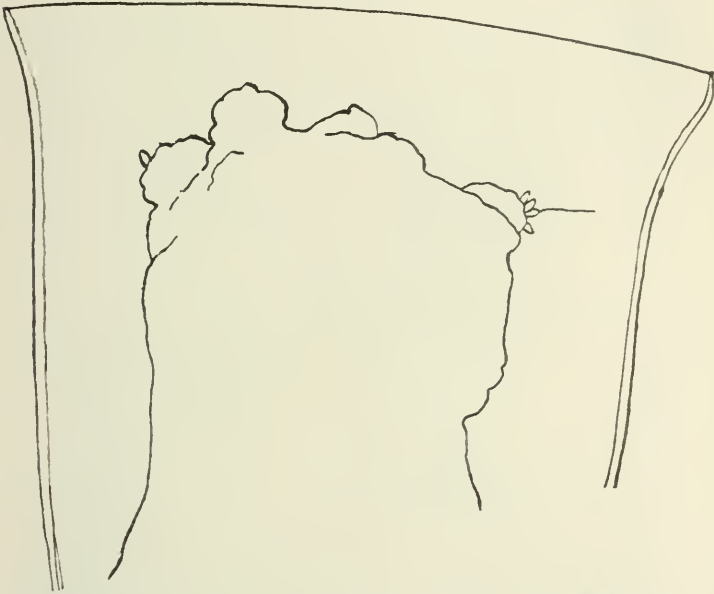
HISTOLOGY.

In the previous section the various stages of resorption were briefly described. The actual route of migration of the cells is, of course, through the gastro-vascular cavity (Pl. 26, figs. 2,

3, and 4). The stream of cells and débris can also be observed directly under the microscope while resorption is going on in the living organism.

The questions remain, how and under what conditions do the resorbed elements start the migration, and where do they eventually get to?

TEXT-FIG. 2.



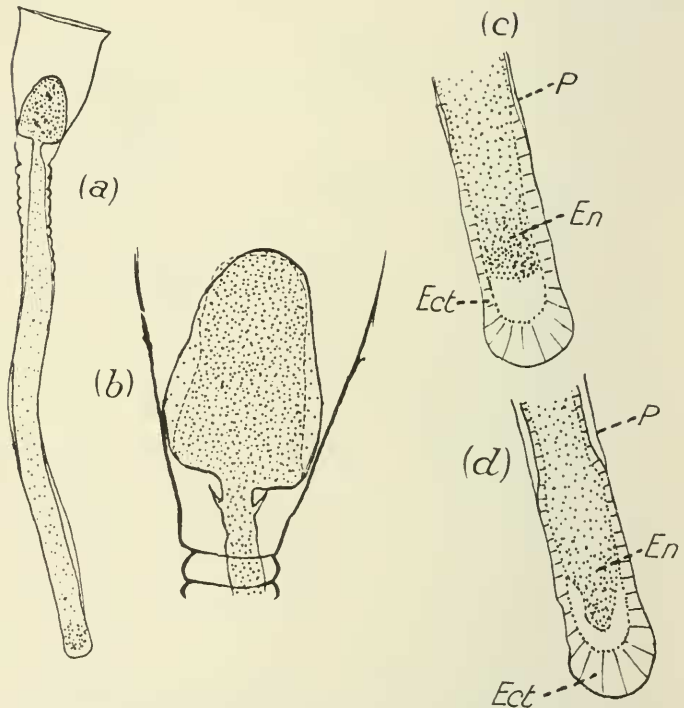
Campanularia. End of stage 2. The hypostome has disappeared, the tentacles are represented only by minute knobs, some almost resorbed. Nematocysts here and there project from the surface of the tentacles, one discharged. (Camera lucida.)

We will first study a tentacle. In the normal zooid the tentacle is almost twice as long as the hypostome, and its axis of endoderm is composed of large cells with very definite walls and flattened like a pile of discs. The endodermal axis occupies more than three-quarters of the diameter of the tentacle (Pl. 26, fig. 6).

In the first stage of resorption the tentacle has shrunk considerably both in length and diameter (Pl. 26, fig. 7). The endo-

derm cells are smaller, and the most distal ones have lost the typical disc-like structure. They are rounded and have lost their serial arrangement in a single row : at the tip it is difficult to dis-

TEXT-FIG. 3.

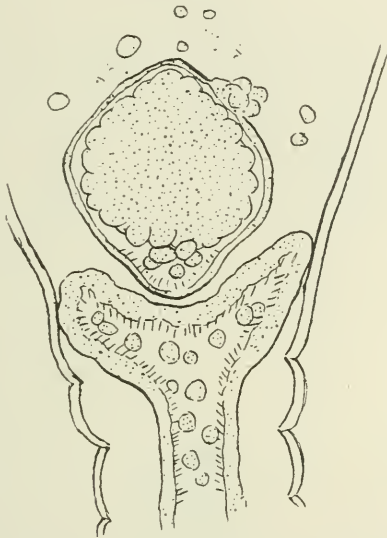


Campanularia. *a*, Stage 3. No trace of tentacles or hypostome. Considerable new growth from the stem. *b*, The same zooid magnified to show its change of shape. The dotted outline was drawn one minute later than the firm outline. *c*, Tip of the new growth from the same specimen in expanded condition. *d*, The same specimen contracted two minutes later. The ectoderm near the tip is attached to the perisare; proximal to this the contraction is clearly visible. *ect.*, ectoderm; *en.*, endoderm; *p.*, perisare. (Camera lucida.)

tinguish them from the ectoderm cells, which have come to present the same spheroidal appearance. Pl. 26, fig. 7, is a photograph of a single section showing progressive loss of differentiation

in the endoderm axis of a tentacle as one approaches the distal extremity. This loss of differentiation gradually extends proximally, and the whole tentacle passes into the gastrovascular cavity after rupture of the mesoglaea (confirming Thacher, 1903). In Pl. 26, fig. 4, the cavity is seen to be filled with cells and débris, the result of resorption of the tentacles.

TEXT-FIG. 4.



Campanularia. The distal part of the zooid has separated from the proximal part. Active cilia occur in both parts, also immigrated cells, but those in the proximal part are sparser as they are migrating down the stem. Some cells of the distal part are migrating outwards. (Camera lucida.)

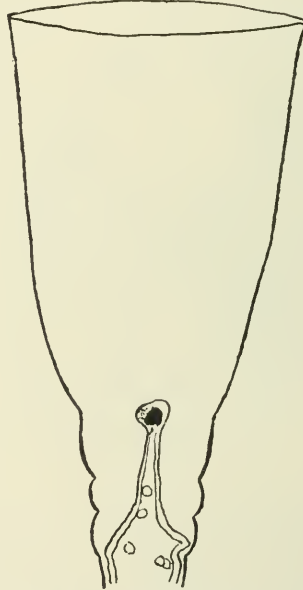
Resorbed elements from the hypostome are no doubt there also, although indistinguishable.

Examined under high powers, it appears that the boundaries of the loose cells in the gastrovascular cavity lose more of their distinctness the farther the elements are from the periphery. The spherical or ovoid bodies to be seen in the centre of the zooids containing refractive matter (but not staining very definitely) are nematocysts. Nearer the periphery

the cells appear as in Pl. 26, fig. 8, still with a definite cell boundary. Nematocysts only appear in the gastrovascular cavity in late stages of resorption, after rupture of the mesoglaea at the base of the tentacles. The bulging in of the basal mesoglaea before breaking is well shown in Pl. 26, fig. 3, left-hand tentacle.

Appearances sometimes occur in *Obelia* which seem to show

TEXT-FIG. 5.



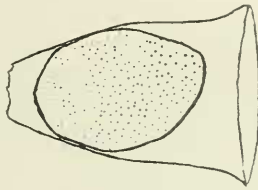
Campanularia. End of stage 4. The zooid is represented only by a small stalked knob containing a mass of pigment, mostly brown with some orange granules. (Camera lucida.)

that phagocytosis is taking place. This was corroborated on a specimen of *Campanularia* (the one shown in Text-fig. 6) which was accidentally ruptured: numerous endoblasts with contained nematocysts were then seen; but in addition, nematocysts were found inside cells much larger than endoblasts; frequently two would be seen within a single large cell (see Text-fig. 7).

Presumably the large cells are endoderm cells which still retain the phagocytic properties normally associated with intracellular digestion.

Occasionally we have noticed in sections of normal specimens appearances indicating the phagocytosis of small (presumably

TEXT-FIG. 6.



Campanularia. Zooid cut off at base of hydrotheca. Dedifferentiation to an ellipsoid mass. Many nematocysts were to be seen in the interior. (Camera lucida.)

TEXT-FIG. 7.

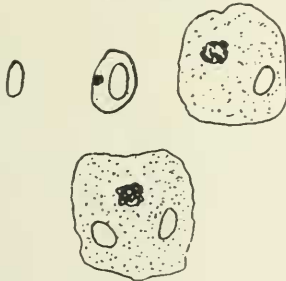


Diagram showing the manner of occurrence of nematocysts in the interior of the zooid shown in Text-fig. 6. (Observations *in vivo*.) The nematocysts were loose, or still in their endoblast, or ingested in a large endoderm cell, or two inside one endoderm cell.

interstitial) cells by normal endoderm cells. Professor G. C. Bourne, F.R.S., has kindly informed us that he has seen similar appearances in *Hydra*, which he also interprets as cases of phagocytosis of one type of cell by another. This process, however, is clearly much commoner in the specimens undergoing resorption than in normal zooids.

It is in any case difficult to see on what occasions phago-

cytosis of the organism's own nematocysts would occur in its normal life-history. It would thus appear that in certain circumstances the power of ingesting food-particles, possessed by certain types of cells, results in typical phagocytosis of other cells of the organism—a process unusual or abnormal for these forms, but usual and normal in higher animals.

Loeb (1900) states that the tentacles fuse in some cases. Thacher (1903) considers this to be only the appearance caused by their being crowded together and by the ectoderm being thrown into folds by excessive contraction. After careful study of serial sections of a zooid in this condition we can state that this explanation will not suffice. The tentacles are, it is true, contracted and crowded, but there is actual fusion in several places (Pl. 26, fig. 9).

The ectoderm cells of the tentacles and hypostome become more cubical during resorption.

Of the endoderm cells, the large mass of glandular cells in the hypostome very soon disappears, the cells passing into the cavity.

In the last stage of resorption before the hydrotheca is evacuated altogether (stage 5), what is left of the zooid is still bounded by a definite epithelium (Pl. 26, fig. 8) of flattened cells, beneath which are others losing their differentiation. The behaviour of the ectoderm cells may be compared with that of a rear-guard, continually retreating yet always maintaining an unbroken front. But as the zooid is resorbed, its volume and surface decrease, and so the front diminishes.

At the start the cavity is not too congested and the cells and debris pass down; but in later stages the cavity is almost blocked up (Pl. 26, fig. 8), and it is then that pulsation can be observed. This obviously facilitates the evacuation. It is presumably due to tension on the walls of the stolon.

In *Obelia* it is possible to observe the cells actually leaving the tissues, a process which has often been taken for granted in other forms (see Pl. 26, fig. 2, left side).

Where do the resorbed elements go when they pass down into the hydrocaulus out of the zooid? It appears that they

are ingested by the endoderm cells of the hydrocaulus, or break down and in that condition are absorbed by those cells.

The walls of the hydrocaulus even in the last stages of resorption appear normal when seen alive under the microscope and in sections, though its cavity may be filled up with cells and débris.

But is it possible that the new growth which takes place at the proximal cut end of the hydrocaulus consists of the very elements derived from the resorbed zooids? Loeb makes the observation that this growth is like the motion of a protoplasmic mass, and such it certainly appears to be in our experiments. But this would be the appearance presented by normal growth proceeding at the rate at which this stolon was produced—10 mm. in forty-eight hours or less.

In structure the new growth is similar to an ordinary piece of hydrocaulus (Text-fig. 3).

This growth starts only after a certain stage of resorption has been reached.

The new growth adheres to the substratum, thus resembling the normal creeping stolon. We were unable to observe whether it could give rise to buds in *Obelia*, as the preparations died. In *Campanularia*, pieces with several zooids might give rise to one or several buds during or after resorption of the original zooid.

DISCUSSION.

Loeb (1900) attributes resorption to contact with solid objects. According to him the transformation must be due to liquefaction of the more solid constituents of the zooid. Contact with the fluid, sea-water, makes for the production of the more solid portion of the colony, the zooid; whereas conversely contact with a hard surface makes for the more fluid stem. Accordingly if a zooid be subjected to the stimulus to which the production of the stem-system is the reaction, the result will be the conversion of the zooid into something resembling the stem.

But resorption of zooids takes place even when the colony is maintained in an erect position and no portion of the zooid

is allowed to touch any hard object (Thacher, 1903). Clearly then, contact cannot be the only cause of resorption. It is rather to be interpreted in terms of equilibrium between two systems with different physiological reactions: if one wishes to use Child's phraseology one may say that they possess different metabolic rates, and the one with the higher rate is, normally, physiologically dominant over the other.

In the case of these hydroids there are two systems, the zooid and the stem (hydrocaulus).

Normally, the more highly differentiated zooid is able to maintain itself, but being more specialized and less plastic than the stem the zooid will not be able to maintain itself in the face of conditions which, though adverse for the zooid, do not appreciably affect the stem. Such are, e. g., a N/256,000 solution of KCN, or laboratory conditions after fifty hours. The result of the adverse conditions is inhibition of normal function; and within limits it is differential, affecting the zooid before and more than the stem.

By interfering with general metabolism, as is done by exposure to toxic agencies, the output of energy is reduced. Energy is needed to maintain differentiated form against surface-tension. Thus one of the first results of non-lethal interference will be the loss of typical form by cells and their reversion to a spheroidal or cuboidal shape. This is found in all cases of dedifferentiation known, and often leads to the assumption of spheroidal form by the whole organism (see Huxley, 1922).

The fact that exposure to laboratory conditions, to KCN and to HgCl_2 , all bring about identical reactions indicates that the effects of the poisons, &c., are not specific, but that all act in a general way, by affecting the energy-production of the tissues.

It may be asked how the process we have called dedifferentiation in *Obelia* differs from simple degeneration. The answer is to be found in observation of the process. At no time can it be said that the zooid is dead: during the whole process of resorption what is left of it is just as alive as the normal zooid or stem. If the zooid dies, as it does if the poisons are too strong, the cells acquire a characteristic semi-opaque appearance

which cannot be mistaken. There is then no more resorption and the cells macerate, and later disintegrate, without dedifferentiation.

Resorption is a result of the process of migration and it could not take place were the elements to be resorbed to remain in their differentiated condition. Resorption then is consequent on dedifferentiation. It occurs in many forms when a cavity is present into which the migration may occur (Child, 1904; Huxley, 1921 *b*).

In *Obelia*, as in *Perophora* and probably in many other cases, if the cavity into which migration can occur be by some method or other limited, dedifferentiation with no or slight resorption may take place (Text-fig. 6, p. 485).

It is then dedifferentiation plus resorption that Loeb means by 'liquefaction'. But this is not a specific result of contact with hard surfaces. Whether such contact by itself can produce the effect we do not know, but as an unfavourable condition it can and does accelerate it. Contact stimulates tentacles to contract, and constant stimulation must be unfavourable; oxidation must also be reduced in proximity to the substratum. Loeb's analogy between the liquefaction of the zooid and the clotting of blood, both due to contact with solid objects, thus cannot stand.

It may be said that dedifferentiation implies potential subsequent redifferentiation. There is, however, no reason why dedifferentiation should be reversible any more than differentiation. If we lay down that dedifferentiation is reversion to a morphologically simpler state with lower energy-requirements, the simpler condition being preserved for a considerable time and not merely a stage in the process of dying, we have a good working definition.

Dedifferentiation is the accepted term to denote the simplificatory processes undergone by differentiated cells in tissue culture; and in this case there is usually no redifferentiation, the tissues merely remaining alive for a longer or shorter time in their simplified condition. Smooth muscle grown in culture solutions dedifferentiates to a condition in which the cells divide

actively (no division normally occurs in adult smooth muscle). If such a preparation be grafted back into its former position it is just possible to arrest the mitoses, but redifferentiation proceeds no further (Champy, 1913). (Strangeways informs us verbally that he has been more successful.) On the other hand, redifferentiation of dedifferentiated tissue has been obtained by Drew (1923) *in vitro*.

Redifferentiation of the zooid was not obtained in *Obelia* as it was in *Clavellina* (Driesch, 1906; Huxley, unpub.), *Pemmaria* (Cerfontaine, 1902), or *Sycon* (Huxley, 1911). But in those cases where redifferentiation does occur, we must ask whether the new adult structure is formed from the redifferentiation of the dedifferentiated cells, or from indifferent cells which have all along retained the full hereditary potentialities. The study of budding and asexual reproduction, especially Hadzi's work (1910) on *Hydra*, suggests that the latter is usually the case. If this is so, then the failure to redifferentiate is in no way due to the inactivity of the dedifferentiated elements, but of the indifferent cells. Vandel (1921), however, shows that in regenerating Planarians (*Polycelis*), the new pharynx is produced from cells of other organs which dedifferentiate and then redifferentiate along new lines, scarcely any mitoses being observed. This is a good example of pluripotent dedifferentiation (Adami and Macrae, 1914; Huxley, 1921 *a*). The usual process, however, in colonial forms, is for the dedifferentiated tissues to provide material for new outgrowths of the nature of stolons, from which later new zooids may arise (cf. Ascidians, Huxley, 1921 *b*; Hydroids, Müller, 1913).

When the metabolic requirements of the zooid have decreased, the equilibrium between it and the stem is upset and the balance is now in favour of the latter (Huxley, 1921 *b*). In the higher animals complete resorption of systems does not usually occur. For one thing the cells are too solidly packed in tissues, and they are usually attacked by phagocytes before they have even had time to be resorbed. But a concurrence of both processes is seen in the absorption of the tail in Ascidian tadpoles. Here, according to Delage and Hérouard (1898), 'ses

éléments se désagrègent,' after which process the phagocytic action commences. Most authors are also agreed that a process of dedifferentiation initiates the resorption of the tail in Anuran tadpoles, phagocytosis being secondary (cf. Naville, 1922).

Phagocytosis here only occurs after resorption, i. e. after the tissue elements have migrated from the tissues. It would appear not to be a normal process in Hydroids, but to be a result of (a) the power of the endoderm cells to ingest solid particles, (b) the presence of abnormally situated cells which have migrated out of the tissues in the neighbourhood of the endoderm cells. Phagocytosis of this nature appears to occur both in the case of emigrated endoderm cells of the zooid, and of normal endoderm cells in the walls of the stem.

Resorption (as a result of emigration of dedifferentiated cells) may be regarded as the most primitive method of eliminating tissues in Metazoa. Even at the outset it may be secondarily accompanied by a low form of phagocytosis. Later the function of phagocytosis is assigned to special cells, and the dedifferentiating tissues are attacked by these at a much earlier stage in the process. The limited extent of phagocytosis in low forms is also to be seen in Planarians (Vandel, 1921).

Resorption is in the first instance a direct result of exposure to unfavourable agencies, but may be utilized later as a method of accomplishing normal processes of the life-history. This appears to be the case in Echinoderm metamorphosis (Huxley, 1922).

The stimulus in the case of *Obelia* is a certain concentration of toxic products in the water. It is the same stimulus which causes dedifferentiation in *Clavellina* and *Perophora*, and also in Echinoderm larvae, Planarians, Sponges, and Protozoa (Lund, 1917).

Hunger is another stimulus which may cause dedifferentiation; and of course may act differentially. Dedifferentiation caused by hunger has been found in *Hydra* (Schultz, 1906), Echinoderm larvae (Rumström, 1917), &c. Starvation will again act by interfering with general metabolic processes. As an example of the differential action of hunger, it may be mentioned that in starved tadpoles, localized dedifferentiation

often takes place in one or more places on the tail (unpublished observations, J.S.H.). Dedifferentiation is not, however, followed by resorption in this case, at least before death.

Müller (1913, 1914) has conducted an elaborate series of experiments with various species of Hydroids. He finds that dedifferentiation and resorption may occur not only in hydranths but also in gonophores and in portions of hydrocaulus. There is a delicately balanced equilibrium between various parts of a system; in a compound system, whether gonophore, hydranth, or stem shall be resorbed depends (a) on the relative sizes and (b) on the ages of the sub-systems (cf. *Perophora*, Huxley, 1921 *b*). Wounds will induce gonophores to dedifferentiate and be resorbed.

The quantitative action of poisons in accelerating dedifferentiation and resorption, and the fact that in severed zooids dedifferentiation may proceed independently of resorption, are points on which we would like to lay stress.

SUMMARY.

1. Confirmation is given of the results of Loeb, Thacher, Godlewski and Gast, and others, in showing that the hydranths of hydroids (in this case *Obelia* and *Campanularia*) when exposed to unfavourable conditions proceed to dedifferentiate and to be resorbed, wholly or mainly, into the stem.

2. Exposure to toxic agencies accelerates the process. Too great concentration of poison kills the zooids before dedifferentiation starts. Below the death-point, the acceleration is proportional to the concentration.

3. The effect is non-specific, both KCN and HgCl₂ producing the same result as prolonged exposure to laboratory conditions.

4. When zooids are separated from the stem, resorption is impossible. Dedifferentiation, however, proceeds until an ovoid undifferentiated body packed with cells is produced.

5. The tentacles are first affected, then the hypostome. In early stages, separate tentacles may fuse locally. Stumps of tentacles are, however, still present after the hypostome has quite disappeared. The body becomes ovoid, then spherical, and is finally reduced to a minute pigmented dot.

6. The surface tension of the dedifferentiated zooid causes the emigrated zooid cells to flow into the stem. In later stages spontaneous pulsations of the stem and of the zooid (these possibly not spontaneous) occur.

7. Dedifferentiation of the tissues of the tentacles starts at the tip. Progressive histological dedifferentiation of the endoderm cells can thus be clearly followed in a single section.

8. Only after the mesoglaea at the base of the tentacle has ruptured can the contents be resorbed (confirming Thacher).

9. Cnidoblasts with nematocysts can be distinguished within the gastrovascular cavity as resorption proceeds. They may also be seen phagocytosed within large cells, presumably immigrated endoderm cells.

10. The dedifferentiation is regarded as due to interference with general metabolic processes, and especially with the production of the energy needed to maintain form against surface-tension.

11. Resorption is regarded as the natural result of dedifferentiation when there are adjacent cavities into which the cells can migrate. In higher forms it has been largely replaced by phagocytosis.

EXPLANATION OF PLATE 26.

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Obelia geniculata.

Fig. 1.—Longitudinal section through a normal zooid. $\times 100$.

Fig. 2.—First stage of resorption. $\times 115$.

Fig. 3.—First stage of resorption (slightly later than Fig. 2). $\times 130$.

Fig. 4.—Third stage of resorption. $\times 146$.

Fig. 5.—Fourth stage of resorption. $\times 240$.

Fig. 6.—A tentacle of a normal zooid showing the differentiation of the endoderm. $\times 300$.

Fig. 7.—A tentacle of a zooid in the first stage of resorption showing beginning of dedifferentiation in the distal endoderm cells. Also note especially the reduction in width of the endoderm cells. $\times 420$.

Fig. 8.—Cells and nematocysts in a zooid in the fourth stage of resorption. $\times 420$.

Fig. 9.—Fusion of tentacles. First stage. $\times 270$.

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